# MONTANE MEADOW PLANT ASSOCIATIONS OF SEQUOIA NATIONAL PARK, CALIFORNIA

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ABSTRACT

Twelve plant associations are recognized and described for montane meadows of Sequoia National Park based on 81 relevés. Three major groups are defined by growth-form dominants: mixed forb and grass associations, *Carex* and *Scirpus* associations, and *Eleocharis* associations. Major environmental factors influencing vegetation distribution include: 1) a complex moisture gradient incorporating water depth and movement, and 2) site exposure and shading. Monitoring of water wells indicates that seasonal fluctuations of the water table are important in structuring the vegetation.

Montane meadows, a common feature of Sequoia National Park in the southern Sierra Nevada of California, punctuate a landscape dominated by mixed conifer forest. Scenic vistas, a rich and colorful flora, proximity to Giant Sequoia groves, and accessibility result in disproportionate public visitation to these sites. Nevertheless, montane meadows in the Park and in the southern Sierra Nevada in general have been poorly described.

Studies of montane meadows and their environmental controls were initiated as part of a comprehensive study of riparian ecosystems and the interactions between terrestrial (forest and meadow) and stream systems in Sequoia National Park. As hydric sites, these montane meadows may be grouped functionally with forest riparian systems. Stream channels, overland flows, and pooled water are common. Plant community physiognomy, composition, and distribution reflect strong seasonal and spatial hydrologic patterns.

Disturbance history and microenvironmental characteristics also influence vegetation composition and structure. It is difficult to assess the degree to which montane meadows in Sequoia National Park are recovering from a history of human and livestock use. Although disturbance currently appears minimal, present-day meadow vegetation may reflect the burning activities of aboriginal man as well as the widespread grazing of sheep and cattle during the late 1800s and early 1900s. The sites studied, however, do not exhibit the characteristics of habitat deterioration (trampling, surface erosion, hummock formation, gullying, and obvious reduction in vegetation cover) reported from many subalpine meadows in the southern Sierra Nevada (Armstrong 1942, Sumner 1941, 1948, Sharsmith 1959, Hubbard et al. 1965, 1966, Harkin and Schultz 1967, Leonard

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et al. 1967, 1968, Giffen et al. 1969). Whereas these studies are qualitative, subsequent studies by Bennett (1965) and Strand (1972) provide a more quantitative basis for the evaluation of disturbance and subsequent plant succession. DeBenedetti and Parsons (1979a) reviewed the history of human and domestic livestock use of meadows in the southern Sierra Nevada, providing examples of subsequent resource problems and evaluating the effectiveness of management actions.

Natural disturbance in the form of lightning fire may play an infrequent yet important role in subalpine meadows of the southern Sierra Nevada, particularly along the forest-meadow ecotone (DeBenedetti and Parsons 1979b, 1984). Natural fire in montane meadows of Sequoia National Park has not been reported in the literature and its historical role is unknown.

The focus of this paper is the composition and distribution of montane meadow plant communities and their relationship to major environmental features in Sequoia National Park. It provides basic information for managers as well as a baseline for future research. The classification presented complements studies of subalpine meadows in the southern Sierra Nevada and in Sequoia National Park in particular (Sumner 1941, Sharsmith 1959, Bennett 1965, Harkin and Schultz 1967, Strand 1972, Ratliff 1979, 1982, Benedict and Major 1982, Benedict 1981, 1983).

## Study Area

Meadows examined were located in the mixed conifer forest zone of Sequoia National Park (Rundel et al. 1977) between 1493 and 2390 m elevation (Fig. 1). Sample plots were concentrated in the Giant Forest area and included Log, Crescent, Circle, Huckleberry, and Round Meadows and Vasey's Paradise; Long, Cahoon, Cabin, and Halstead Meadows were sampled outside the *Sequoiadendron* groves. Ten unnamed meadows were sampled and two additional sites were included from Kings Canyon National Park.

Forest composition surrounding meadow sites varies. *Pinus ponderosa, P. lambertiana, Abies concolor, A. magnifica* var. *shastensis, Calocedrus decurrens,* and *Sequoiadendron giganteum* are the most common tree species within the closed canopy forests. Understory dominants include *Chrysolepis sempervirens, Ceanothus cordulatus,* and *Pteridium aquilinum.* A variety of herbs comprise only minimal cover in the ground layer. Forest-meadow ecotones are abrupt both in vegetation and environment; tree encroachment is minimal.

Long-term climatic records are available for the Giant Forest (elevation 1966 m) (Parsons and DeBenedetti 1979). The regional climate is Mediterranean with warm, relatively dry summers and cool wet winters. Hydric montane meadows, however, are less in-

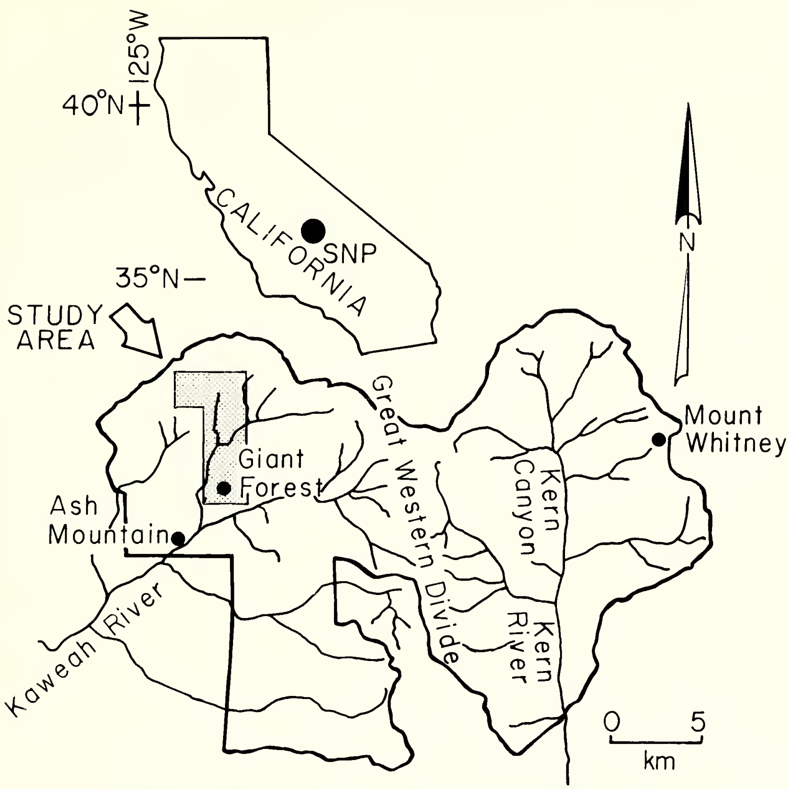


FIG. 1. Location of the study area in Sequoia National Park, California.

fluenced by regional climate than are surrounding forests, as they receive surface as well as sub-surface water throughout the growing season. Although average annual precipitation is 113 cm, June through September averages less than 3 cm (Rundel 1972); most precipitation occurs from December to March as snow. Mean annual snowfall at the Giant Forest exceeds 500 cm and depths of greater than 2 m are common in mid-winter. The average date when mountain basins are free of snow is May 20 (Wood 1975). Average minimum temperatures range from −6.7°C in February to 11.8°C in August. Average maximum temperatures range from 3.4°C in December and January to 27.4°C in August (Parsons and DeBenedetti 1979).

## METHODS

*Vegetation sampling.* Field sampling was conducted during September 1982 using a modification of the reconnaissance method of

Franklin et al. (1970). A total of 81 plots in 20 meadows was sampled. Each plot was located subjectively in an area of visually homogeneous vegetation and habitat. Although the shape varied to accommodate vegetation patterns, plots were most often circular and located within larger areas of similar vegetation to minimize edge effects. Sample plot areas were 250–500 $m^2$; homogeneous units smaller than this were not sampled. Areas of recent natural or man-caused disturbance as well as areas that lacked visually uniform topographic or hydrologic features also were avoided. For each plot visual estimates of projected crown cover were recorded for each vascular plant species. Cover estimates also were made of the various substrate types (bedrock, loose rock, mineral soil, coarse and fine litter, and moss). Environmental features such as elevation, slope, aspect, landform, topography, and hydrologic characteristics also were recorded. Field notes included descriptions of the following: 1) sample plot species composition and physiognomy, 2) hydrologic regime, 3) neighboring vegetation, 4) surrounding forest vegetation, and 5) apparent forest-meadow ecotone changes (seedling and sapling encroachment, meadow expansion, or forest to meadow treefall). Voucher specimens of unidentified species were collected for identification and incorporation into the Oregon State University Herbarium (OSC). Nomenclature of vascular plants follows Munz (1959, 1968). Nomenclature of mosses follows Lawton (1971).

*Vegetation analysis.* Vegetation data were analyzed using two complementary approaches: cluster analysis and ordination analysis. Cluster analysis utilized indicator species analysis (Hill et al. 1975) using the computer program TWINSPAN (Hill 1979a) and manual table sorting techniques (Mueller-Dombois and Ellenberg 1974, Westhoff and van der Maarel 1978). Ordination analysis utilized correspondence analysis (Hill 1973, 1974) as implemented by the program DECORANA (Hill 1979b, Hill and Gauch 1980). Both TWINSPAN and DECORANA are part of the Cornell Ecology Program Series; other programs were developed at Oregon State University (B. G. Smith, unpublished programs).

TWINSPAN is a hierarchical, polythetic, divisive classification technique that uses reciprocal averaging (RA) to produce a classification of samples and species based on differential species. DECORANA is an eigenvector ordination technique derived from reciprocal averaging that attempts to correct two problems of RA—an arch distortion effect and a compression of the axis ends relative to the axis middle (Gauch 1982). An octave transformation of species cover values was performed to compress the range of abundance. The octave scale is logarithmic (base 2) and the transformation prevents the few very abundant species from dominating the analysis.

Montane meadow plant associations were delineated based upon the correspondence of TWINSPAN clusters with manual table sorting results. Ten of the initial 81 samples were ecotonal or outlier stands and could not be assigned successfully to a recognizable association. Because only one sample was available for each, designation at the association level was not justified. Subsequently, the ecotonal and outlier samples were excluded from DECORANA ordination analysis. Associations were plotted on ordination axes and a final classification was developed based upon subjective consideration of group homogeneity with field observations.

*Water table sampling.* To assess seasonal water table fluctuations in a variety of vegetation types, 16 permanent perforated PVC pipe water wells (15 cm diameter) were established along a transect line perpendicular to the long axes of Log and Crescent Meadows, Giant Forest. Wells were placed subjectively in homogeneous vegetation representing selected plant associations. A meter stick was lowered to the water surface to establish depth from ground level. Biweekly measurements of water table depth were taken from 6 July through 8 November 1983.

## Results and Discussion

### Floristic Analysis

A total of 116 vascular plant species and 6 bryophyte genera were identified within the montane meadow sample plots of Sequoia National Park. The vascular flora included 38 families and 77 genera. The 10 families with the greatest number of species are presented in Table 1. The Gramineae had the largest number of genera (14) and species (18). The Cyperaceae was represented by 3 genera and 17 species, and the Compositae by 9 genera and 12 species. Canopy cover of the Cyperaceae, however, dominates these meadows due to the prominence of *Carex, Scirpus,* and *Eleocharis* species. Species with the greatest frequency of occurrence in the samples (constancy) are listed in Table 2. *Oxypolis occidentalis* (Umbelliferae) is nearly ubiquitous, with 78% constancy and 25% characteristic cover (average cover for only those plots in which the species occurs) (Pakarinen 1984). Other important species include *Scirpus microcarpus, Glyceria elata, Eleocharis montevidensis,* and *Carex rostrata,* with constancies of 47 to 60% and characteristic covers of 13 to 20%. Species such as *Athyrium filix-femina, Carex amplifolia,* and *Vaccinium occidentale* are relatively uncommon, but are diagnostic of particular plant associations, and often dominate cover therein.

### Vegetation Analysis

Twelve plant associations and one phase are recognized from the montane meadows of Sequoia National Park. These are grouped

TABLE 1. TEN VASCULAR PLANT FAMILIES WITH THE GREATEST NUMBER OF SPECIES.

| Family | Genera | Species |
|---|---|---|
| Gramineae | 14 | 18 |
| Cyperaceae | 3 | 17 |
| Compositae | 9 | 12 |
| Scrophulariaceae | 4 | 6 |
| Juncaceae | 2 | 5 |
| Liliaceae | 4 | 4 |
| Salicaceae | 1 | 4 |
| Orchidaceae | 3 | 3 |
| Umbelliferae | 3 | 3 |
| Polygonaceae | 2 | 3 |

into three broad types based on growth-form dominants (Table 3): mixed forb and grass associations, *Carex* and *Scirpus* associations, and *Eleocharis* associations. The association concept used herein refers to a recurring assemblage of plant species with visually homogeneous composition and physiognomy representing a modal position in the pattern of vegetation, and, possibly, environment. Association names reflect the diagnostic and often dominant species. Phase names represent recognizable variation in an association attributed to the presence of one or more species.

Species constancy and characteristic cover are compared between plant associations in Tables 4–6. Only species exceeding 49% constancy in at least one association have been included for ease in interpretation. Stand tables containing constancy and characteristic cover statistics for all sample plots within an association are available from the author. Within the following descriptions of associations, "channeled flows" refers to perennial stream courses, "overland flows" refers to unrestricted, generally seasonal runoff across meadow surfaces, "pooled and standing water" refers to relatively still water above the soil surface, and "stagnant water" refers to water not subject to movement at or above the soil surface.

A. MIXED FORB AND GRASS TYPES. Six plant associations comprise the Mixed Forb and Grass Types. A mixture of herbaceous perennials or grass species, or both, dominate these sites, although *Scirpus microcarpus* is occasionally abundant (Table 4). Typically, the Mixed Forb and Grass Types occur in the drier portions of montane meadows.

1. *Glyceria elata–Lotus oblongifolius* Association. This is an herb-rich association with a mosaic appearance. Local dominance of individual species within the mosaic is not accompanied by observable differences in microenvironment; the patterning is likely the result

TABLE 2. TWENTY MOST COMMON MONTANE MEADOW SPECIES, RANKED BY CONSTANCY. [1]Growth-form key: K = herb, G = grass, and S = sedge or rush. [2]Characteristic cover represents the average cover for only those samples in which the species occurs.

| Species | Growth-form[1] | Constancy (%) | Characteristic cover (%)[2] |
|---|---|---|---|
| *Oxypolis occidentalis* | H | 77.8 | 25.2 |
| *Glyceria elata* | G | 60.5 | 7.3 |
| *Scirpus microcarpus* | S | 55.6 | 20.0 |
| *Lotus oblongifolius* | H | 55.6 | 3.5 |
| *Eleocharis montevidensis* | S | 53.1 | 16.5 |
| *Veratrum californicum* | H | 50.6 | 21.7 |
| *Carex rostrata* | S | 46.9 | 13.7 |
| *Dodecatheon jeffreyi* | H | 45.7 | 5.2 |
| *Epilobium exaltatum* | H | 44.4 | 0.5 |
| *Stachys albens* | H | 44.4 | 4.7 |
| *Polygonum bistortoides* | H | 42.0 | 1.3 |
| *Carex nebrascensis* | S | 38.3 | 7.9 |
| *Juncus oxymeris* | S | 34.6 | 2.9 |
| *Senecio triangularis* | H | 32.1 | 3.3 |
| *Habenaria dilatata* | H | 32.1 | 0.2 |
| *Deschampsia caespitosa* | G | 29.6 | 2.6 |
| *Perideridia parishii* | H | 29.6 | 1.7 |
| *Cinna latifolia* | G | 29.6 | 0.8 |
| *Agrostis scabra* | G | 27.2 | 1.9 |
| *Castilleja miniata* | H | 27.2 | 0.7 |

TABLE 3. MONTANE MEADOW PLANT ASSOCIATIONS OF SEQUOIA NATIONAL PARK. Association acronyms are indicated in parentheses.

Mixed Forb and Grass Types

1. *Glyceria elata–Lotus oblongifolius* Association (GLEL–LOOB)
2. *Elymus glaucus–Heracleum lanatum* Association (ELGL–HELA)
3. *Agrostis scabra* Association (AGSC)
4. *Glyceria elata–Scirpus microcarpus* Association (GLEL–SCMI)
5. *Calamagrostis canadensis–Scirpus microcarpus* Association (CACA–SCMI)
6. *Athyrium filix-femina* Association (ATFI)

*Carex* and *Scirpus* Types

7. *Scirpus microcarpus–Oxypolis occidentalis* Association (SCMI–OXOC)
8. *Carex amplifolia–Oxypolis occidentalis* Association (CAAM–OXOC)
9. *Carex nebrascensis–Oxypolis occidentalis* Association (CANE–OXOC)
10. *Carex rostrata* Association (CARO2)

*Eleocharis* Types

11a. *Eleocharis montevidensis–Oxypolis occidentalis* Association, *Eleocharis montevidensis* Phase (ELMO–OXOC–ELMO Phase)
11b. *Eleocharis montevidensis–Oxypolis occidentalis* Association, *Carex rostrata* Phase (ELMO–OXOC–CARO2 Phase)
12. *Eleocharis montevidensis*–Moss Association (ELMO–MOSS)

TABLE 4. CONSTANCY AND AVERAGE COVER SYNTHESIS TABLE FOR THE ASSOCIATIONS OF THE MIXED FORB AND GRASS TYPES. [1]See Table 3 for association acronyms. [2]CON = constancy (%), [3]COV = average cover (%) based only on those samples in which species occurs.

| Plant association[1]: | GLEL–LOOB | | ELGL–HELA | | AGSC | | GLEL–SCMI | | CACA–SCMI | | ATFI | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of plots per type: | 4 | | 5 | | 3 | | 6 | | 4 | | 5 | |
| Mean number of species per plot (s.d.): | 25.0 (6.4) | | 13.4 (5.3) | | 20.7 (2.9) | | 14.0 (2.7) | | 10.5 (5.7) | | 19.6 (2.2) | |
| | CON[2] | COV[3] | CON | COV | CON | COV | CON | COV | CON | COV | CON | COV |
| Herb species | | | | | | | | | | | | |
| *Pteridium aquilinum* | 75 | 3 | — | — | — | — | — | — | — | — | 20 | T |
| *Botrychium multifidum* | 75 | 1 | — | — | — | — | — | — | — | — | 20 | 2 |
| *Senecio clarkianus* | 100 | 5 | 40 | 2 | 67 | 1 | 67 | 5 | 50 | 6 | — | — |
| *Solidago canadensis* | 75 | 31 | 100 | 13 | 67 | 14 | 50 | 23 | 75 | 3 | — | — |
| *Castilleja miniata* | 100 | 4 | 40 | 2 | 33 | 1 | 17 | 2 | — | — | 60 | 1 |
| *Lotus oblongifolius* | 100 | 12 | 20 | 2 | 67 | 9 | 33 | 1 | — | — | 60 | 2 |
| *Sidalcea ranunculacea* | 75 | 12 | 20 | 1 | 100 | 4 | 17 | 1 | 25 | 2 | 40 | 1 |
| *Heracleum lanatum* | — | — | 100 | 19 | — | — | 50 | 2 | 25 | T | 20 | T |
| *Veratrum californicum* | 100 | 6 | 40 | 1 | 100 | 1 | 67 | 11 | 75 | 14 | 60 | 3 |
| *Stachys albens* | 75 | 8 | 100 | 10 | 100 | 13 | 100 | 19 | 50 | 23 | 80 | 5 |
| *Senecio triangularis* | 75 | 10 | 80 | 26 | 33 | 1 | 50 | 6 | — | — | 100 | 22 |
| *Epilobium exaltatum* | 50 | 2 | 60 | 2 | 100 | 1 | 83 | 1 | 50 | 1 | 60 | 1 |
| *Viola glabella* | 75 | 1 | — | — | — | — | 33 | 1 | 25 | 2 | 60 | 9 |
| *Lupinus latifolius* | 50 | 3 | 40 | 2 | 33 | 2 | — | — | 25 | T | 80 | 4 |
| *Oxypolis occidentalis* | 75 | 2 | — | — | 67 | 5 | 17 | 8 | 50 | 3 | 100 | 13 |
| *Habenaria dilatata* | 75 | 1 | — | — | — | — | 17 | 1 | 25 | T | 100 | 2 |
| *Mimulus guttatus* | — | — | 20 | 3 | 33 | T | 50 | 7 | — | — | 60 | 1 |
| *Athyrium filix-femina* | 25 | T | 20 | 1 | — | — | 17 | 1 | — | — | 100 | 72 |
| Grass species | | | | | | | | | | | | |
| *Elymus glaucus* subsp. *jepsonii* | 100 | 3 | — | — | 67 | T | — | — | — | — | — | — |
| *Elymus glaucus* subsp. *glaucus* | 75 | 2 | 100 | 47 | 33 | 5 | 67 | 3 | 50 | 1 | — | — |
| *Phleum pratense* | 75 | 3 | — | — | 100 | 20 | 50 | 1 | 25 | 1 | — | — |

TABLE 4. CONTINUED.

| Plant association[1]: | GLEL–LOOB | | ELGL–HELA | | AGSC | | GLEL–SCMI | | CACA–SCMI | | ATFI | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of plots per type: | 4 | | 5 | | 3 | | 6 | | 4 | | 5 | |
| Mean number of species per plot (s.d.): | 25.0 (6.4) | | 13.4 (5.3) | | 20.7 (2.9) | | 14.0 (2.7) | | 10.5 (5.7) | | 19.6 (2.2) | |
| | CON[2] | COV[3] | CON | COV | CON | COV | CON | COV | CON | COV | CON | COV |
| *Agrostis scabra* | 50 | 3 | 40 | 1 | 100 | 43 | 67 | 2 | 25 | 7 | — | — |
| *Poa pratensis* | — | — | — | — | 67 | 2 | 17 | 1 | — | — | — | — |
| *Calamagrostis canadensis* | 25 | T | 60 | 27 | — | — | — | — | 100 | 55 | — | — |
| *Glyceria elata* | 100 | 5 | 80 | 5 | 100 | 2 | 100 | 49 | 100 | 15 | 100 | 16 |
| *Cinna latifolia* | 25 | 5 | 40 | 2 | — | — | 50 | 1 | — | — | 100 | 5 |
| Sedge and rush species | | | | | | | | | | | | |
| *Juncus oxymeris* | 50 | 9 | — | — | 67 | 1 | 17 | 10 | — | — | — | — |
| *Carex leporinella* | 25 | 7 | 20 | 3 | 67 | 46 | 17 | 1 | — | — | 60 | 2 |
| *Scirpus microcarpus* | 25 | 2 | 60 | 7 | 100 | 2 | 83 | 66 | 100 | 51 | 60 | 26 |
| *Carex feta* | — | — | — | — | 67 | 1 | 17 | T | — | — | 20 | T |

of initial establishment and vegetative spread of rhizomatous perennial forbs. Species of greatest constancy and cover include *Lotus oblongifolius, Senecio clarkianus, Castilleja miniata, Solidago canadensis,* and *Glyceria elata.* Species of Cyperaceae occur occasionally, but are more common on wetter sites. This association is common along meadow edges and on elevated flats in the driest portions of montane meadows.

2. *Elymus glaucus–Heracleum lanatum* Association. This association is characterized by a dominance of *Elymus glaucus* and a host of perennial forbs, including *Heracleum lanatum, Solidago canadensis, Stachys albens,* and *Senecio triangularis.* Floristic composition is similar to the *Glyceria elata–Lotus oblongifolius* Association, but dominance has shifted to grasses. This association occurs along montane meadow edges and on elevated flats where the water table falls well below the soil surface throughout the growing season.

3. *Agrostis scabra* Association. This association is limited to small areas in several montane meadows. It resembles the two mixed forb and grass associations described previously, but also has abundant *Agrostis scabra. Phleum pratense* is a common grass associate, whereas *Stachys albens, Solidago canadensis,* and *Lotus oblongifolius* are common herbs. This association is restricted to drier, convex landforms that have a relatively deep water table. The abundance of *Agrostis scabra* and *Phleum pratense* suggest previous disturbance on these sites.

4. *Glyceria elata–Scirpus microcarpus* Association. *Glyceria elata* reaches its peak abundance within this association, and *Scirpus microcarpus* is a codominant. *Stachys albens* is a consistent associate and *Solidago canadensis* and *Veratrum californicum* are locally common. These sites typically exhibit channeled or overland water flows.

5. *Calamagrostis canadensis–Scirpus microcarpus* Association. *Calamagrostis canadensis* and *Scirpus microcarpus* exceed 100% total canopy cover in this species-poor association. *Glyceria elata* is the only other species with 100% constancy. This association commonly occurs near meadow edges on moist to saturated sites adjacent to channeled or overland flows.

6. *Athyrium filix-femina* Association. A nearly complete upper canopy of the fern *Athyrium filix-femina* characterizes this association. *Senecio triangularis* and *Oxypolis occidentalis* are common, as are the grasses *Glyceria elata* and *Cinna latifolia.* This association is restricted to narrow, cool, and shaded meadows that are commonly the smaller basin swales in which forest canopy shading is important. It also can occur in modified form as streamside vegetation where forest canopies are relatively dense. These sites typically have saturated soils, and seeps are common.

B. *Carex* and *Scirpus* types. Four plant associations comprise the *Carex* and *Scirpus* Types. Sites are typically dominated by *Scirpus microcarpus,* or coarse-leaved species of *Carex,* or both (Table 5). Species richness is generally low. These associations occupy areas with pooled, channeled, or overland flows.

7. *Scirpus microcarpus–Oxypolis occidentalis* Association. Height and density of the vegetation suggest that this type has the highest standing crop of any montane meadow type. *Scirpus microcarpus* reaches greatest abundance in this association; *Oxypolis occidentalis* is an important codominant; and *Athyrium filix-femina, Stachys albens, Mimulus guttatus,* and *Equisetum arvense* are frequent associates. This vegetation type is widespread, usually occurring along stream channels and within areas of overland flow where the water table remains at or above the soil surface throughout the growing season.

8. *Carex amplifolia–Oxypolis occidentalis* Association. This association is restricted to small, shaded, swale meadows similar to those supporting the *Athyrium filix-femina* Association. *Carex amplifolia* dominates these sites and *Oxypolis occidentalis* is of secondary importance. Common associates include *Glyceria elata, Cinna latifolia, Athyrium filix-femina, Mimulus guttatus,* and *Cardamine breweri.* Soils typically are saturated throughout the growing season.

9. *Carex nebrascensis–Oxypolis occidentalis* Association. *Carex nebrascensis* reaches peak abundance in this association, whereas *Oxypolis occidentalis, Carex rostrata,* and *Eleocharis montevidensis* are codominant species. This vegetation type is related compositionally and structurally to the *Eleocharis montevidensis–Oxypolis occidentalis* type. Habitats typically are flat to gently sloping; pooled to slightly-flowing water is present throughout the growing season.

10. *Carex rostrata* Association. This association occurs under a variety of topographic and hydrologic regimes. Under deeply-pooled water, pure stands of *Carex rostrata* develop. On sloping sites or under conditions of decreased water tables, *C. rostrata* abundance and vigor decrease and species diversity increases. The common associated herbs include *Dodecatheon jeffreyi, Polygonum bistortoides, Oxypolis occidentalis,* and *Perideridia parishii.* Moss can be locally abundant.

C. *Eleocharis* types. Two plant associations and one phase comprise the *Eleocharis* Types. Typically, sites are dominated by the fine-stemmed spike-rush, *Eleocharis montevidensis* (Table 6). Standing or nearly stagnant water at or above the soil surface is characteristic of these communities.

11a. *Eleocharis montevidensis–Oxypolis occidentalis* Association, *Eleocharis montevidensis* Phase. This association resembles the *Carex nebrascensis–Oxypolis occidentalis* Association; however, *Carex*

TABLE 5. CONSTANCY AND AVERAGE COVER SYNTHESIS TABLE FOR THE ASSOCIATIONS OF THE *Carex* AND *Scirpus* TYPES. [1]See Table 3 for association acronyms. [2]CON = constancy (%). [3]COV = average cover (%) based only on those samples in which species occurs.

| Plant association[1]: | SCMI–OXOC | | CAAM–OXOC | | CANE–OXOC | | CARO2 | |
|---|---|---|---|---|---|---|---|---|
| Number of plots per type: | 7 | | 2 | | 10 | | 5 | |
| Mean number of species per plot (s.d.): | 17.6 (4.7) | | 15.0 (1.4) | | 11.6 (4.9) | | 10.6 (6.5) | |
| | CON[2] | COV[3] | CON | COV | CON | COV | CON | COV |
| Herb species | | | | | | | | |
| *Lupinus latifolius* | 71 | 2 | — | — | — | — | — | — |
| *Senecio triangularis* | 71 | 1 | 50 | T | — | — | — | — |
| *Mimulus guttatus* | 71 | 4 | 100 | 9 | — | — | — | — |
| *Cardamine breweri* | 43 | 1 | 100 | 3 | — | — | — | — |
| *Athyrium filix-femina* | 86 | 5 | 100 | 5 | 10 | T | — | — |
| *Stachys albens* | 71 | 16 | 100 | 2 | 10 | T | — | — |
| *Viola glabella* | 57 | 1 | — | — | — | — | 20 | 5 |
| *Lilium kelleyanum* | 57 | T | — | — | 20 | T | 20 | T |
| *Veratrum californicum* | 57 | 3 | 50 | 15 | 40 | 4 | 20 | 1 |
| *Epilobium exaltatum* | 57 | 1 | 100 | 2 | 20 | 1 | 40 | 3 |
| *Lotus oblongifolius* | 71 | 2 | 50 | 3 | 40 | 2 | 40 | 9 |
| *Equisetum arvense* | 57 | 17 | — | — | 70 | 3 | — | — |
| *Oxypolis occidentalis* | 100 | 47 | 100 | 33 | 90 | 66 | 60 | 7 |
| *Polygonum bistortoides* | 14 | T | — | — | 70 | 2 | 60 | 10 |
| *Dodecatheon jeffreyi* | 14 | 3 | — | — | 40 | 4 | 60 | 22 |
| *Perideridia parishii* | — | — | — | — | 10 | T | 60 | 7 |
| Grass species | | | | | | | | |
| *Cinna latifolia* | 86 | 3 | 100 | 2 | 10 | 1 | — | — |
| *Glyceria elata* | 100 | 7 | 100 | 7 | 40 | 4 | 20 | T |
| *Deschampsia caespitosa* | 14 | 1 | — | — | 30 | T | 60 | 6 |

TABLE 5. CONTINUED.

| Plant association[1]: | SCMI–OXOC | | CAAM–OXOC | | CANE–OXOC | | CARO2 | |
|---|---|---|---|---|---|---|---|---|
| Number of plots per type: | 7 | | 2 | | 10 | | 5 | |
| Mean number of species per plot (s.d.): | 17.6 (4.7) | | 15.0 (1.4) | | 11.6 (4.9) | | 10.6 (6.5) | |
| | CON[2] | COV[3] | CON | COV | CON | COV | CON | COV |
| Sedge and rush species | | | | | | | | |
| *Carex amplifolia* | 14 | 7 | 100 | 83 | — | — | — | — |
| *Scirpus microcarpus* | 100 | 79 | — | — | 50 | 30 | 40 | 5 |
| *Eleocharis montevidensis* | 29 | 2 | 100 | 4 | 90 | 20 | 60 | 6 |
| *Carex nebrascensis* | 14 | 2 | — | — | 100 | 42 | 40 | 9 |
| *Carex rostrata* | 29 | 3 | — | — | 90 | 25 | 100 | 79 |

TABLE 6. CONSTANCY AND AVERAGE COVER SYNTHESIS TABLE FOR THE ASSOCIATIONS OF THE *Eleocharis* TYPES. [1]See Table 3 for association acronyms. [2]CON = constancy (%). [3]COV = average cover (%) based only on those samples in which species occurs.

| Plant association[1]: | ELMO–OXOC CARO2 PHASE | | ELMO–OXOC ELMO PHASE | | ELMO–MOSS | |
|---|---|---|---|---|---|---|
| Number of plots per type: | 2 | | 5 | | 13 | |
| Mean number of species per plot (s.d.): | 16.0 (11.3) | | 16.6 (6.8) | | 19.1 (4.8) | |
| | CON[2] | COV[3] | CON | COV | CON | COV |
| Shrub species | | | | | | |
| *Vaccinium occidentale* | — | — | — | — | 54 | 15 |
| Herb species | | | | | | |
| *Habenaria dilatata* | — | — | 60 | 1 | 15 | T |
| *Veratrum californicum* | 50 | 1 | 60 | 1 | 15 | T |
| *Lotus oblongifolius* | 100 | 13 | 60 | 5 | 69 | 3 |
| *Oxypolis occidentalis* | 100 | 41 | 100 | 62 | 100 | 17 |
| *Dodecatheon jeffreyi* | 100 | 15 | 60 | 7 | 100 | 15 |
| *Camassia leichtlinii* | 50 | 3 | 60 | T | 69 | 1 |
| *Perideridia parishii* | 50 | T | 40 | 3 | 92 | 8 |
| *Polygonum bistortoides* | — | — | 60 | T | 69 | 3 |
| *Hypericum anagalloides* | — | — | 20 | 7 | 54 | 9 |
| *Spiranthes romanzoffiana* | — | — | 20 | T | 62 | 1 |
| *Mimulus primuloides* | — | — | — | — | 69 | 21 |
| *Aster alpigenus* | — | — | — | — | 85 | 5 |
| Grass species | | | | | | |
| *Glyceria elata* | 50 | 1 | 60 | 2 | 8 | T |
| *Deschampsia caespitosa* | 50 | 1 | — | — | 62 | 8 |
| *Muhlenbergia filiformis* | — | — | — | — | 69 | 8 |
| Sedge and rush species | | | | | | |
| *Scirpus microcarpus* | 100 | 8 | 60 | 19 | 15 | 23 |
| *Carex rostrata* | 100 | 45 | 60 | 2 | 69 | 15 |
| *Juncus oxymeris* | 100 | 5 | 80 | 2 | 77 | 17 |
| *Eleocharis montevidensis* | 100 | 63 | 100 | 66 | 100 | 46 |
| *Carex nebrascensis* | — | — | 60 | 5 | 62 | 15 |
| *Carex ormantha* | — | — | — | — | 69 | 9 |
| Bryophyte species | | | | | | |
| *Sphagnum/Philonotis/ Aulacomnium* | 50 | 4 | 60 | 13 | 92 | 64 |

is less important and *Eleocharis* assumes dominance. Although species richness can be high, few species have constancies greater than 60%. The physiognomy is two-layered, having a tall *Oxypolis* overstory and an open *Eleocharis* understory. Water remains at or slightly above the soil surface throughout the growing season.

11b. *Eleocharis montevidensis–Oxypolis occidentalis* Association, *Carex rostrata* Phase. This uncommon phase occurs on habitats with slightly higher standing or flowing water regimes than the typical community. The physiognomy is similarly two-layered, but the understory is denser due to the abundance of *Carex rostrata. Eleocharis montevidensis* and *Oxypolis occidentalis* are dominant, and *Dodecatheon jeffreyi* and *Lotus oblongifolius* are common herbs.

12. *Eleocharis montevidensis*–Moss Association. This association is characterized by 1) a moss mat composed primarily of *Sphagnum, Philonotis,* and *Aulacomnium,* occurring singly or in combination; 2) an abundance of *Eleocharis*; and 3) a characteristic mosaic of mat-forming vascular species such as *Aster alpigenus, Hypericum anagalloides, Mimulus primuloides,* and *Muhlenbergia filiformis. Juncus oxymeris* and *Perideridia parishii* are taller diagnostic associates. The average cover of moss is 60%. Standing to stagnant surface water typifies level sites whereas surface seeps typify sloping sites.

## Relation to Other Sierra Nevada and Cascade Meadows

Several meadow associations of Sequoia National Park are similar structurally and, in certain instances, floristically to montane meadows found elsewhere in the Sierra Nevada and in the Cascade Range of Oregon.

The physiognomy and floristic character of the *Eleocharis montevidensis*–Moss Association tie it to many montane mire systems throughout the Sierra Nevada and the Oregon Cascade Range. The complex of matted-boggy species with a taller, open *Eleocharis* layer is characteristic. *Eleocharis pauciflora* is the diagnostic counterpart in the montane zone of the Cascade Range and in the subalpine zone of the southern Sierra Nevada. Within the Sierra, Benedict (1981, 1983) describes an *Eleocharis pauciflora* Association and an *Eleocharis pauciflora–Mimulus primuloides* variant from the Rock Creek and Whitney Creek drainages of Sequoia National Park. Similarly, Ratliff (1979, 1982) defines an *Eleocharis pauciflora* type (few-flowered spike-rush/Site Class H) within the subalpine zone of Yosemite, Sequoia, and Kings Canyon National Parks, and the Stanislaus, Sierra, and Sequoia National Forests. In the Western Cascades of Oregon, Hickman (1976) alludes to a phase of his Bog Association that may have a similar assemblage of low-growing herbs. Halpern et al. (1984) describe similar vegetation, defined as the *Eleocharis pauciflora* community type, within the Three Sisters Wilderness Area, Oregon. An *Eleocharis pauciflora*/bryophyte community at Sphagnum Bog, Crater Lake National Park, Oregon (very similar in composition and physiognomy to that in Sequoia National Park), is described by Seyer (1979). At Multorpor Fen, Mt. Hood National

Forest, Oregon, Seyer (1983) also describes an *Eleocharis*/herbs/*Aulacomnium–Sphagnum* community, which is a similar low stature, moss-mat community with permanently saturated soils. Campbell (1973) describes an *Eleocharis–Aulacomnium* community at Hunts Cove, Mt. Jefferson, Oregon, within a larger *Carex scopulorum* meadow complex.

The *Carex nebrascensis–Oxypolis occidentalis* and the *Carex rostrata* Associations, typical of standing to slightly flowing water regimes in montane meadows of Sequoia National Park, have analogues elsewhere. Ratliff (1979, 1982) describes a Nebraska sedge class (Site Class G) common on nearly level, imperfectly to moderately well-drained, subalpine sites in the southern Sierra Nevada. *Carex nebrascensis*- and *Carex rostrata*-dominated vegetation is described from Grass Lake, California, by Beguin and Major (1975). Benedict (1981, 1983) describes a subalpine *Carex rostrata–Mimulus primuloides* Association from the Whitney and Rock Creek drainages of Sequoia National Park. It appears similar to the herb-rich variant of the montane *Carex rostrata* association of the Park, occurring on sites with depressed water tables. Ratliff (1979, 1982) describes a *Carex rostrata* type (beaked sedge/Site Class A) occupying poorly and imperfectly drained sites. *Carex rostrata* assemblages are also important in many hydric montane meadows throughout the Oregon Cascade Range. Campbell (1973) describes a *Carex rostrata–Sphagnum* community at Hunts Cove, Mt. Jefferson, Oregon. *Carex rostrata*-dominated reedswamps at Sphagnum Bog, Crater Lake National Park, and Gold Lake Bog near Willamette Pass, Oregon, have been described by Seyer (1979). A *Carex rostrata* community with *C. sitchensis* has been reported for Big Springs near Nash Crater, Oregon (Roach 1958). Frenkel (pers. comm.) identifies similar reedswamp vegetation at Torrey Lake Mire, Oregon. Comparable assemblages are scattered throughout the Three Sisters Wilderness Area, Oregon, under standing to slightly flowing water conditions.

Several associations of the Mixed Forb and Grass Types within the montane meadows of Sequoia National Park contain herb species common to meadows of the Sierra Nevada and Oregon Cascade Range. The particular compositions and physiognomies of these assemblages, however, may be specific to the Park. This uncertainty reflects the paucity of reports of similar associations in the montane and subalpine meadow literature. Similarly, basin swale communities dominated by *Athyrium filix-femina* may represent a rather unique aspect of montane meadows in Sequoia National Park. Although the fern is common in coastal forested swamps in Oregon and Washington (Franklin and Dyrness 1973) and along mountain streams in the Cascade Range and Sierra Nevada, extensive meadow swards have not been described outside of Sequoia National Park.

The prominence of *Oxypolis occidentalis* is perhaps the most unique floristic aspect of the montane meadows of Sequoia National Park. A tall, leafy umbel of marshy meadows and shallow water, *Oxypolis* ranges from Tulare Co. to Eldorado Co. in the Sierra Nevada, and north to Crater Lake in Oregon (Jepson 1936). It has been reported as a fairly common component of only two geographically limited hydric communities in the subalpine of the southern Sierra Nevada and at Crater Lake National Park (Ratliff 1979, Seyer 1979). In contrast, in montane meadows of Sequoia National Park, *Oxypolis* occurs in 11 of 12 associations and dominates in nearly half of these. In most cordilleran wet meadows, graminoids are the sole dominants, but in similar communities in Sequoia National Park, *Oxypolis occidentalis* plays a significant role as a codominant.

## Detrended Correspondence Analysis

The results of the detrended correspondence analysis are useful in describing vegetation patterns and inferring complex environmental gradients (Fig. 2). The overlay of TWINSPAN groups on the ordination reveals the spatial relationship between associations within the two dimensional compositional space portrayed. Interpretation of these axes as environmental gradients is possible if we consider stand compositions, species autecology, and environmental information.

DCA ordination yielded the four eigenvalues of 0.63, 0.31, 0.19, and 0.16, which suggest that only the first two axes are important. The first eigenvector, or axis of the ordination, is 4.6 standard deviation units long, representing a moderate turnover in species composition within samples along that gradient (Gauch 1982). Field observations suggest this axis represents a complex moisture gradient that incorporates water table depth and water movement. The driest representatives of this gradient (toward the left end of Axis 1) are the *Elymus glaucus–Heracleum lanatum, Glyceria elata–Lotus oblongifolius,* and *Agrostis scabra* Associations. They typify sites with seasonal lowering of the sub-surface water table. Located more centrally along Axis 1 is vegetation that typifies channeled or flowing water sites—the *Scirpus microcarpus–Oxypolis occidentalis* Association is a representative. To the right of these are associations that exhibit shallow to deep and standing to slightly flowing water throughout the growing season. Included are both phases of the *Eleocharis montevidensis–Oxypolis occidentalis* Association, the *Carex rostrata* Association, and the *Carex nebrascensis–Oxypolis occidentalis* Association. To the extreme right lies the *Eleocharis montevidensis*–Moss Association typical of sites with persistent, standing to stagnant, surface water.

The second DCA axis is not as easily interpreted as the first. The

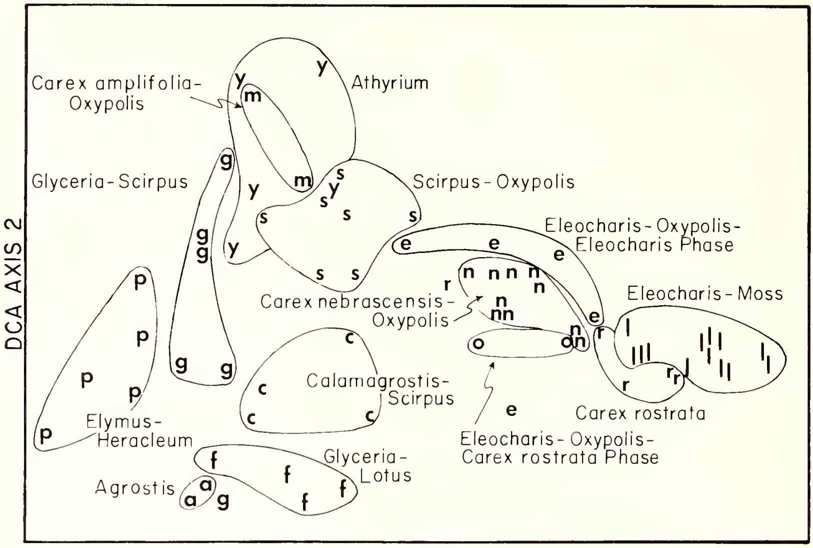


FIG. 2. Detrended correspondence analysis ordination of samples. Letters indicate samples representing the same association, as defined in Table 3.

axis is 2.8 standard deviation units long, representing a significantly smaller turnover in species composition than along Axis 1. The forb–grass associations in the left portion of the ordination space have a better separation than the *Carex* and *Eleocharis* Associations to the right. Field observations suggest that at its ends, the axis seems to describe extremes in meadow exposure and shading, reflecting site location in one of two broad landform classes: 1) within small concave openings or swales in mixed conifer forest or in *Sequoiadendron* groves, where bordering trees provide much shade; or 2) in large, broad basins of greater area and minimal shading.

Typical swale vegetation occurs highest on Axis 2 and is represented by the *Carex amplifolia–Oxypolis occidentalis* and *Athyrium filix-femina* Associations. At the other extreme, open basin vegetation (represented by the *Agrostis scabra* and *Glyceria elata–Lotus oblongifolius* Associations) occurs lowest on Axis 2. Those types with intermediate positions along Axis 2 (the *Glyceria elata–Scirpus microcarpus* and *Scirpus microcarpus–Oxypolis occidentalis* Associations) occur over a wider range of habitats. They are found within more shaded sites in swale, stringer, or streamside meadows, as well as within large, open meadow basins. The *Calamagrostis canadensis–Scirpus microcarpus* Association has affinities to the *Glyceria elata–Lotus oblongifolius* Association as it is restricted to open basins. The former usually occurs farther from drier edges and closer to drainage channels and areas of overland flow than the latter.

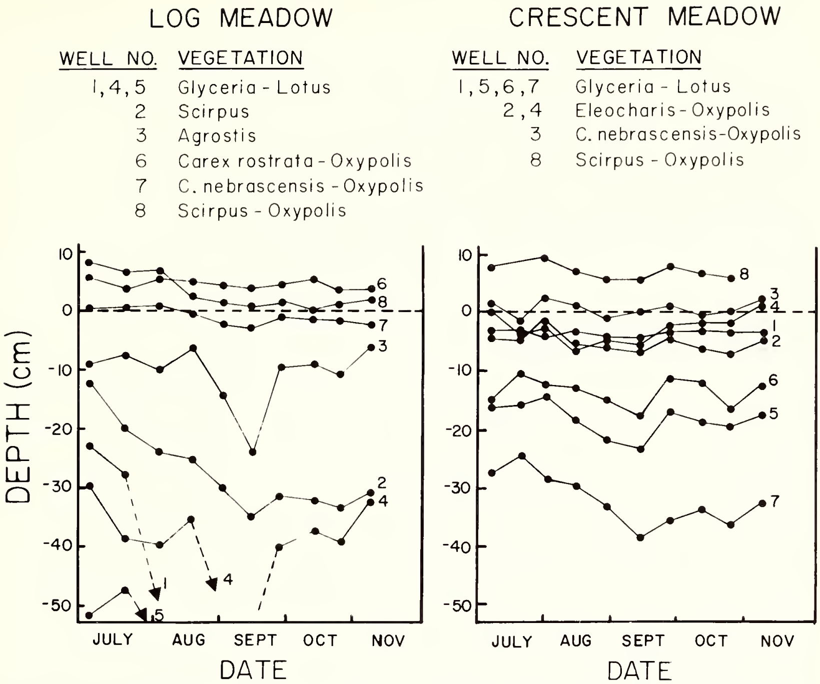


FIG. 3. Water table depths for Log and Crescent Meadows, Giant Forest, for 6 Jul to 8 Nov 1983.

## Water Table Dynamics

Species distributions and vegetation composition largely reflect meadow hydrology. Detrended correspondence analysis ordination indicates that plant associations segregate along a complex moisture gradient reflecting water table depth and movement. Results from seasonal water table measurements reinforce this interpretation (Fig. 3). Although the water table patterns represent only two meadow sites for a single growing season during a year with an unusually high snow-pack and greater than average summer rains, the distribution of vegetation nevertheless reflects spatial differences in meadow hydrology.

Several general trends are evident from the water well transects in Log and Crescent Meadows. Water was progressively drawn down from 6 July through 12 September in those communities that experienced a fluctuating water regime (see Fig. 3, *Glyceria elata–Lotus oblongifolius* Association, Wells 1, 4, 5, Log Meadow; *Glyceria elata–Lotus oblongifolius* Association, Wells 5, 6, 7, Crescent Meadow; and *Agrostis scabra* Association, Well 3, Log Meadow). In several instances, the water table fell below well bottoms (see arrows, Fig.

3). Small but distinct increases in the water table during the period of decline may correspond to summer rains (8–10 August, 1.5 cm; 15–19 August, 4.0 cm). From 12 September through final sampling on 8 November, the water table progressively increased to levels that were near initial sampling heights in most areas even though fall rains had been minimal (approximately 7.1 cm from 22 September to 8 November). Apparently enough water remains within side-slopes to restore the water table to early summer levels when evapotranspiration is reduced during senescence of late summer vegetation. Wood (1975) described similar patterns in a subalpine meadow at the Central Sierra Snow Laboratory.

Rates of decline and increase in the water table were variable across meadow transects; maximum rates of change appeared in the *Agrostis scabra* community of Log Meadow. Here, levels dropped an average of 0.21 cm per day through mid-September and rose an average of 0.25 cm per day through early November. Wood (1975) reported a stronger water table rise, 1.2 cm per day, in his subalpine meadow.

Water wells located more centrally in the meadows (in vegetation dominated by *Scirpus microcarpus–Oxypolis occidentalis, Carex rostrata–Oxypolis occidentalis, Carex nebrascensis–Oxypolis occidentalis,* and *Eleocharis montevidensis–Oxypolis occidentalis*) showed minor fluctuations in growing season water depths. These were communities with water essentially at or above the soil surface throughout the sampling period. *Eleocharis montevidensis–Oxypolis occidentalis* sites (Wells 2, 4, Crescent Meadow) showed minor water table fluctuations of 1 to 2 cm. The *Carex nebrascensis*-dominated sites (Well 7, Log Meadow, and Well 3, Crescent Meadow) maintained water levels between −0.5 and +2.0 cm. *Scirpus microcarpus*-dominated sites exhibited standing water tables as great as 9 cm, but levels slowly declined to 0.5 and 5.0 cm by September (Well 8, Log Meadow, and Well 8, Crescent Meadow, respectively). The *Carex rostrata* site maintained a stable, standing water table at 2.0–3.0 cm (Well 6, Log Meadow).

A *Scirpus microcarpus* site near a stream channel in Log Meadow (Well 2) appeared anomalous in that water table fluctuations resembled those more characteristic of *Glyceria elata–Lotus oblongifolius* meadow edge communities. Its occurrence on elevated coarse sand deposits may explain the rather large 17 cm depression of the water table from 6 July through 12 September. Patterns within a *Glyceria elata–Lotus oblongifolius* site in Crescent Meadow (Well 1) also appeared anomalous as the water table remained stable beneath the soil surface through the growing season. Unusually high winter snowpack and August rainfall may be masking more distinct water table patterns in these meadows, particularly in communities with permanently saturated soils. Typically, the water table in these sites may drop both differentially, and more quickly to lower mid-summer depths. Nevertheless, seasonal measurements, field observations, and ordination results suggest the importance of water depth and movement in montane meadow vegetation patterns.

## Conclusion

The analysis of montane meadow vegetation in Sequoia National Park complements similar research within subalpine meadows of the southern Sierra Nevada and provides baseline data for future research and management. Twelve plant associations and one phase are segregated floristically, reflecting environmental variation in 1) water table depth and water movement, and 2) site exposure and shading. Vegetation similar floristically and physiognomically to that described herein exists elsewhere in the Sierra Nevada and in the western Cascade Range of Oregon. Although spatial and seasonal patterns of water depth and movement influence the composition and distribution of plant communities, future research is necessary to address the relative importance of microenvironmental parameters and disturbance.

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## Literature Cited

Armstrong, J. E. 1942. A study of grazing conditions in the Roaring River District, Kings Canyon National Park, with recommendations. National Park Service Report.

Beguin, C. and J. Major. 1975. Contribution a l'etude phytosociologique et ecologique des marais de la Sierra Nevada (Californie). Phytocoenologia 2:349–367.

Benedict, N. B. 1981. The vegetation and ecology of subalpine meadows of the southern Sierra Nevada, California. Ph.D. dissertation, Univ. California, Davis.

———. 1983. Plant associations of subalpine meadows, Sequoia National Park, California. Arctic and Alpine Research 15:383–396.

——— and J. Major. 1982. A physiographic classification of subalpine meadows of the Sierra Nevada, California. Madroño 29:1–12.

Bennett, P. 1965. An investigation of grazing impact of 10 meadows in Sequoia-Kings Canyon National Park. M.A. thesis, San Jose State College, California.

Campbell, A. G. 1973. Vegetative ecology of Hunts Cove, Mt. Jefferson, Oregon. M.S. thesis, Oregon State Univ., Corvallis.

DeBenedetti, S. and D. J. Parsons. 1979a. Mountain meadow management and research in Sequoia and Kings Canyon National Parks: a review and update. *In* R. L. Linn, ed., Proceedings of the First Conference on Scientific Research in the National Parks. U.S.D.I. Nat. Park Serv. Trans. and Proc. Series No. 5. Washington, DC 2:1305–1311.

——— and ———. 1979b. Natural fire in subalpine meadows: a case description from the Sierra Nevada. J. Forest. (Washington) 77:477–479.

——— and ———. 1984. Post-fire succession in a Sierran subalpine meadow. Amer. Midl. Naturalist 111:118–125.

Franklin, J. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. Forest Serv. Gen. Techn. Rept. PNW-8.

———, ———, and W. H. Moir. 1970. A reconnaissance method for forest site classification. Shinrin Richi (Tokyo) 12:1–14.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge.

Giffen, A., C. M. Johnson, and P. Zinke. 1969. Ecological study of meadows in Lower Rock Creek, Sequoia National Park (unpubl.).

Halpern, C. B., B. G. Smith, and J. F. Franklin. 1984. Composition, structure, and distribution of the ecosystems of the Three Sisters Biosphere Reserve/Wilderness Area. Report to the U.S.D.A.

Harkin, D. W. and A. M. Schultz. 1967. Ecological study of meadows in Lower Rock Creek, Sequoia National Park. Progress report for 1966 (unpubl.).

Hickman, J. C. 1976. Non-forest vegetation of the central western Cascade Mountains of Oregon. Northw. Sci. 50:145–155.

Hill, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61:237–249.

———. 1974. Correspondence analysis: a neglected multivariate method. Applied Statistics 23:340–354.

———. 1979a. TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics, Cornell Univ., Ithaca, NY.

———. 1979b. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell Univ., Ithaca, NY.

———, R. G. H. Bunce, and M. W. Shaw. 1975. Indicator species analysis, a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland. J. Ecol. 63:597–613.

——— and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58.

Hubbard, R. L., C. E. Conrad, A. W. Magill, and D. L. Neal. 1966. The Sequoia National Park and Pacific Southwest Forest Range Exp. Sta. cooperative mountain meadow study. Part II: An ecological study of Lower Funston Meadow (unpubl.).

———, R. Riegelhuth, H. R. Sanderson, A. W. Magill, D. L. Neal, R. H. Twiss, and C. E. Conrad. 1965. A cooperative study of mountain meadows. Part I: Extensive survey and recommendations for further research (unpubl.).

Jepson, W. L. 1936. A flora of California. Vol. 2. California School Book Depository, San Francisco.

Lawton, E. 1971. Moss flora of the Pacific Northwest. The Hattori Botanical Laboratory, Nichinan, Japan.

Leonard, R., D. Harkin, and P. Zinke. 1967. Ecological study of meadows in Lower Rock Creek, Sequoia National Park. Progress report for 1967 (unpubl.).

———, C. M. Johnson, P. Zinke, and A. Schultz. 1968. Ecological study of meadows in Lower Rock Creek, Sequoia National Park. Progress report for 1968 (unpubl.).

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. Wiley, NY.

Munz, P. A. 1959. A California flora. Univ. California Press, Berkeley.
———. 1968. Supplement to a California flora. Univ. California Press, Berkeley.
Pakarinen, P. 1984. Cover estimation and sampling of boreal vegetation in northern Europe. *In* R. Knapp, ed., Handbook of vegetation sampling: methods and taxon analysis in vegetation science, p. 35–44. W. Junk, The Hague, Netherlands.
Parsons, D. J. and S. H. DeBenedetti. 1979. Impact of fire suppression on a mixed conifer forest. Forest Ecol. Manage. 2:21–33.
Ratliff, R. D. 1979. Meadow sites of the Sierra Nevada, California. Classification and species relationships. Ph.D. dissertation, New Mexico State Univ., Las Cruces.
———. 1982. A meadow site classification for the Sierra Nevada, California. U.S.D.A. Forest Serv. Pacific Southw. Forest Range Exp. Sta., Gen. Techn. Rept. PSW-60.
Roach, A. W. 1958. Phytosociology of the Nash Crater lava flows, Linn County, Oregon. Ecol. Monogr. 22:169–193.
Rundel, P. W. 1972. Habitat restriction in Giant Sequoia: the environmental control of grove boundaries. Amer. Midl. Naturalist 87:81–95.
———, D. J. Parsons, and D. T. Gordon. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 559–599. Wiley-Interscience, NY.
Seyer, S. C. 1979. Vegetation ecology of a mountain mire, Crater Lake National Park, Oregon. M.S. thesis, Oregon State Univ., Corvallis.
———. 1983. Ecological analysis of Multorpor Fen Preserve, Oregon. Report to the The Nature Conservancy.
Sharsmith, C. W. 1959. A report on the status, changes and ecology of back country meadows in Sequoia and Kings Canyon National Parks (unpubl.).
Strand, S. 1972. An investigation of the relationship of pack stock to some aspects of meadow ecology for seven meadows in Kings Canyon National Park. M.S. thesis, California State Univ., San Jose.
Sumner, E. L. 1941. Special report on range management and wildlife protection in Kings Canyon National Park (unpubl.).
———. 1948. Tourist damage to mountain meadows in Sequoia-Kings Canyon National Park 1935–1948. A review with recommendations (unpubl.).
Westhoff, V. and E. van der Maarel. 1978. The Braun-Blanquet approach. W. Junk, The Hague, Netherlands.
Wood, S. H. 1975. Holocene stratigraphy and chronology of mountain meadows, Sierra Nevada, California. Ph.D. dissertation, California Institute of Technology, Pasadena.

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